An *in vivo* Comparative Study of Intersegmental Flexibility in the Ophiuroid Arm

ELIZABETH E. LeCLAIR[1,*] AND MICHAEL C. LaBARBERA[2]

[1]*Committee on Evolutionary Biology and* [2]*Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th Street, Chicago, Illinois 60637*

Abstract. We present the first *in vivo* measurements of intersegmental rotation in the ophiuroid arm, comparing lateral bending performance in seven epifaunal species from Discovery Bay, Jamaica. The species studied include suspension-feeders, deposit-feeders, and scavengers, and also represent two major types of vertebral ossicle morphology. Animals were photographed with strobe illumination, and the angular deflections between arm segments were recorded. Despite considerable variation in vertebral morphology, ecology, and behavior, Discovery Bay ophiuroids show similar, overlapping distributions of maximal intersegmental rotations. Although interspecific differences in mean lateral flexibility can be statistically significant, absolute differences among species are small and of unknown functional significance. These quantitative data challenge long-standing assumptions about how the ophiuroid vertebral skeleton affects intersegmental flexibility, and how intersegmental flexibility *per se* affects an ophiuroid's ecological style or success.

Introduction

The echinoderm skeleton, like all skeletal systems, constrains and directs the actions of the animal. The skeletal ossicles can be connected rigidly, as in the echinoid test, or flexibly, as in the mobile appendages of crinoids, asteroids, and ophiuroids. Each type of connec-

tion imposes certain biomechanical limits on organismal form and function. Only a few of these systems, however, have been studied in detail (crinoids: Meyer, 1973; Macurda and Meyer, 1976; Donovan, 1988; Riddle *et al.*, 1988; Holland *et al.*, 1991; Baumiller *et al.*, 1991; Baumiller and LaBarbera, 1993; echinoids: Telford, 1985; Ellers and Telford, 1991; Carnevali *et al.*, 1991, 1993; asteroids: Eylers, 1976; O'Neill, 1989).

The behavior and ecology of ophiuroids are thought to be influenced by the mobility of their heavily calcified, multisegmented arms (Fig. 1). Externally, the ophiuroid arm is covered with a regular arrangement of overlapping plates or scales. Internally, the arm contains a series of disk- or rod-shaped vertebral ossicles that articulate with one another proximally and distally, forming a central "spine" that allows the arm to bend under muscular control (for review, see Byrne, 1994). Coordinated motion at numerous intervertebral joints gives the ophiuroid arm an exceptional range of flexibility, as seen in many locomotory and food-gathering behaviors (Fell, 1966; Magnus, 1967; Pentreath, 1970; Warner, 1982; for review, see Lawrence, 1987). Although the shape of the vertebral ossicle is widely presumed (see below) to affect intervertebral rotation, intersegmental flexibility, and thus the potential behavior and ecology of the animal, the range of vertebral morphologies is little studied and their effects remain largely untested.

Ophiuroids are the most ecologically diverse echinoderm class, encompassing predatory, scavenging, suspension-feeding and deposit-feeding lifestyles (for reviews, see Warner, 1982; Lawrence, 1987). This "high ecological adaptability" (Litvinova, 1989a) has been attributed to the evolutionary innovation of the vertebral ossicle system, which presumably allowed increased arm
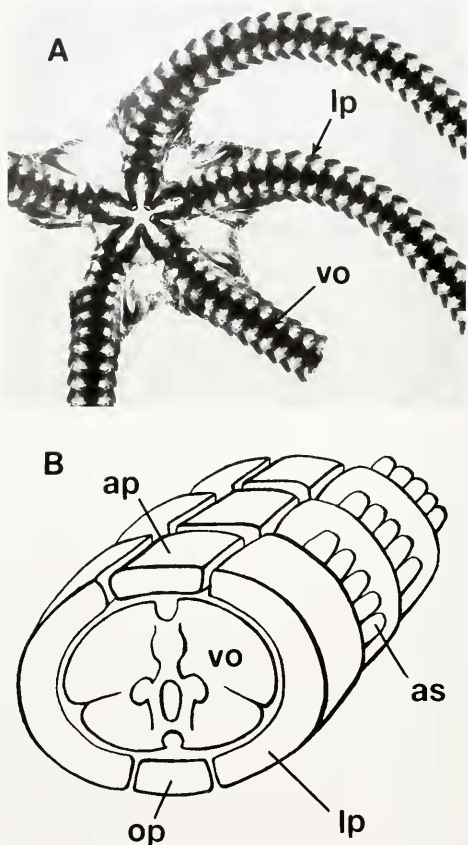
Figure 1. Anatomical overview of the ophiuroid arm skeleton. (A) X-ray view showing segmentation of the arms and the internal series of vertebral ossicles (*Ophioderma cinereum*). (B) Diagrammatic cross-section of the arm showing the relationships of internal and external skeletal plates. ap = aboral plate, as = arm spine, lp = lateral plate, op = oral plate, vo = vertebral ossicle.

mobility (Spencer and Wright, 1966) and the subsequent "radiation" of vertebral ossicle morphologies within the established arm skeleton. Thus vertebral variations among both living and fossil ophiuroid taxa are often described as mechanical adaptations for different lifestyles or behaviors (Berry, 1934; Litvinova, 1989a,b).

Such variations have long been noted (Lyman, 1882; Bell, 1892; Matsumoto, 1915, 1917), and recent research has explored the taxonomic distribution and functional implications of different vertebral ossicle forms (Emson

and Wilkie, 1982; Robbins, 1986; Bray, 1988; Byrne and Hendler, 1988; Litvinova, 1989a,b; Hendler and Miller, 1991; LeClair, 1994, 1995, 1996). These descriptive studies generally focus on the shape of the intervertebral articulation, which is often assumed to influence rotation between arm segments. Each vertebral ossicle has two articulation surfaces, one proximal and one distal. In basket stars (order Euryalae), these surfaces have an hourglass-shaped, streptospondylous articulation, which allows the arm to coil helically for maintaining posture and obtaining food (Macurda, 1976; Hendler and Miller, 1984; Dearborn *et al.*, 1986; Emson *et al.*, 1991). Other taxa (order Ophiurae) show a more complex zygospondylous articulation, in which each surface bears a bilaterally symmetrical set of projections and depressions (Fig. 2). The zygospondylous joint is assumed to be more limited in motion, rotating primarily in a lateral plane (Hyman, 1955; Byrne, 1994). The ophiurans are taxonomically and ecologically more diverse than the euryalans, a fact attributed to greater diversity in the configuration of the zygospondylous joint (*e.g.*, Hendler and Miller, 1991).

Interspecific variations in ophiuran vertebral ossicle morphology have been linked to unusual forms of locomotion (Hendler and Miller, 1991) and to specific feeding strategies (Robbins, 1986). Emson and Wilkie (1982) interpreted certain vertebral features in the Amphiuridae, Ophiactidae, and Ophiothricidae as modifications for increased flexibility and postural control, and concluded that "arm structure may be correlated with habit, and also with habitat" (p. 17). Bray (1988) described differences between the vertebral ossicles of *Ophiocoma echinata* and *Ophiothrix suensonii*, and how these variations might influence arm movement and ecology. Hendler and Miller (1991) suggested that reduced articular surfaces in certain *Ophiothrix* might allow a greater range of motion between arm segments, facilitating open-water swimming behavior. The most detailed discussions of the functional morphology of the vertebral ossicle system are by Litvinova (1989a,b; 1994), who inferred mechanical consequences for a variety of vertebral ossicle types.

The ophiuroid literature thus contains many working hypotheses about the biomechanics of the intervertebral articulation, its influence on intersegmental flexibility, and how this flexibility may correlate with ecologically interesting behavior. These hypotheses generally assume (1) that the degree of bending between arm segments depends on the morphology of the intervertebral articulation and (2) that the behavior or ecology of the animal depends on the degree of bending between arm segments. Although structural differences are thus used to explain interspecific differences in intersegmental flexi-
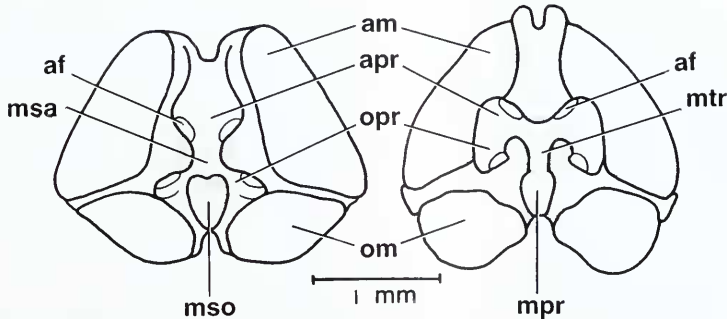
Figure 2. Proximal (left) and distal (right) articulating surfaces of a zygospondylous vertebral ossicle. af = articulating facet, am = aboral muscle area, apr = aboral process, mpr = median process, msa = median saddle, mso = median socket, om = oral muscle area, opr = oral process. Diagram and descriptive terminology slightly modified from Bray (1985).

bility and ecology, no study has quantified the relative flexibility of different ophiuroid arm joints.

Here we report the first comparative assessment of ophiuroid intersegmental flexibility *in vivo*. The first goal of our investigation was to measure intersegmental rotations in live, unrestrained animals representing seven ophiurid families and two major vertebral ossicle morphologies. The second goal was to explore how any differences in observed flexibility might correlate with vertebral ossicle shape, taxonomic group, or dominant feeding mode of the animal. If vertebral ossicle morphology is the primary factor dictating intersegmental flexibility, species with very different vertebral morphologies are predicted to show measurable differences in intersegmental rotations. Conversely, without evidence for interspecific variation in arm performance at the level of the segment, it is unnecessary to invoke differences in vertebral morphology as a causal or adaptive explanation.

Materials and Methods

Experimental animals

Epifaunal ophiuroids were collected from backreef areas at Discovery Bay Marine Laboratories, Discovery Bay, Jamaica (March–April 1995; Fig. 3A). This area supports at least 15 species of ophiuroids, representing 7 families in the order Ophiurae (Sides, 1981). Animals were captured by hand during snorkel and scuba surveys at four sites previously described by Sides (1981) and at a fifth location immediately north of the laboratory's rock jetty (Fig. 3B). Large individuals of *Ophioderma cinereum* were abundant at the latter site, and *Ophiothrix oer-*

stedii was also common. Several individuals of *Ophiothrix suensonii* were collected by scuba divers at Red Buoy Reef in the eastern half of the bay (depth = 18–20 m). Unlike the backreef taxa, which tend to be cryptic during the day, this species was usually conspicuous: individuals could be seen resting, with several arms exposed, in the mouths of large cup sponges.

Live ophiuroids were transferred immediately to running seawater tables for the duration of the field session (2–3 weeks). All animals appeared healthy and active and no arm autotomy was observed. To prevent the animals from becoming acclimated to light, the seawater tables were kept dark with black plastic curtains. No food was added to the tanks, but small particles and sediment were introduced by the constant flow of seawater. All ophiuroids were allowed to adjust for at least 24 h before they were used in any behavioral experiments. Table I lists the species collected, the number of individuals used, and the size of each individual as measured by disk diameter (in millimeters).

The taxa studied also represent a diversity of feeding strategies, including scavenging (*Ophioderma appressum, O. cinereum*), deposit-feeding (*Ophiocoma pumila*), obligate suspension-feeding (*Ophiothrix oerstedii, O. suensonii*), and facultative deposit-/suspension-feeding (*Ophiocoma echinata, O. pumila*). These behavioral categorizations are drawn from previous studies of the same species at the same locality (Sides, 1981, 1984; Sides and Woodley, 1985). Table II lists the vertebral ossicle morphologies and predominant feeding strategies of the species sampled. Two vertebral types, keeled and non-keeled, are represented. A detailed description of these types and an analysis of variation within types is
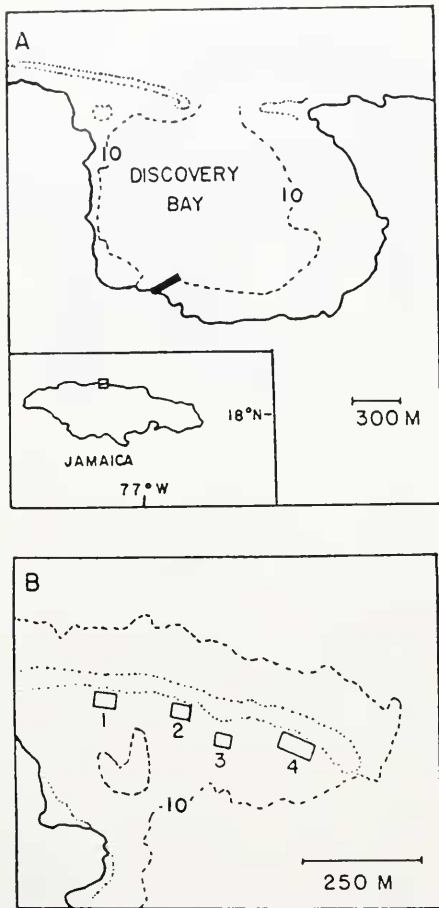
Figure 3. Map of Discovery Bay, Jamaica (from Sides, 1981). (A) Overview of the bay. Dotted line = 10-meter depth contour. (B) Detail of the western half of the bay showing backreef collecting sites (1–4).

given elsewhere (LeClair, 1994, 1995, 1996; see also Robbins, 1986; Smith *et al.*, 1995). In contrast to non-keeled vertebral ossicles (Fig. 4A), keeled vertebral ossicles have reduced articulating projections, a large notch on the proximal aboral surface, and an aboral, distal-pointing projection, or "keel" (Fig. 4B). Each distal keel fits into the proximal notch of the adjacent vertebral ossicle, creating an overlapping, or "imbricated," skeletal series that non-keeled morphs lack (Fig. 4C). Keeled taxa

also feature "accessory aboral muscles" between the proximal depression and distal keel that are absent in non-keeled taxa (Fig 4B; Robbins, 1986). This dichotomy in skeletal structure led us to predict that species with different vertebral ossicle morphologies would show measurable differences in intersegmental flexibility — specifically, that the reduced articular surfaces and additional muscles present in keeled species would allow greater lateral bending, as proposed by Hendler and Miller (1991).

Photographic apparatus

Intersegmental flexibility was recorded by photographing unrestrained ophiuroids moving in a shallow glass aquarium ($30 \times 23 \times 8$ cm). A front-surface mirror was mounted underneath the aquarium, angled 45° to the tank bottom. A Nikon 6006 camera equipped with a macro lens was aimed at this mirror to provide a view perpendicular to the tank floor and the oral surface of the animal. Two Vivitar strobe lights were angled upwards beneath the tank to briefly (1/10,000 s) illuminate the animal from below during each exposure (1/125 s). All exposures were recorded on Kodak Tech Pan film (ASA 25). Images obtained by this method show excellent detail of the oral arm surface and good contrast at the boundaries between external plates (Fig. 5).

Arm-flexing behaviors

All experiments were conducted in a darkened laboratory after dusk (1830–0200 h) when these species are most active (Sides, 1981). Ophiuroids generally show negative phototaxis, rapidly crawling away from any light source. This tendency was exploited to elicit two types of arm-flexing behaviors in the laboratory:

Coiling: One ophiuroid was placed in the center of the tank next to a small, slightly concave rock or coral chip. Most animals, with some prodding, quickly occupied this artificial crevice. Once inside, the ophiuroid was illuminated from above by a small 40-watt incandescent lamp. In response to the light, the animal would generally shelter its disk under the crevice and quickly retract its arms, forming multiple arm loops. When the animal had arranged itself into a stable configuration of coiled arms (after 1–5 min), the camera shutter was fired, triggering the strobes. The incandescent light was then extinguished, the covering rock removed, and the animal allowed to roam freely in darkness for 2–3 min before another trial. Ten trials were recorded for each individual.

Locomotion: One ophiuroid would be gently dropped upside down in the center of the tank, exposed to a faint illumination from one side. The animal would right itself and, using rhythmic arm strokes, walk away from the

Table I

Body disk diameters (±1 mm) for Discovery Bay ophiuroids

	Species						
	Ophiocoma echinata	*Ophioderma cinereum*	*Ophioderma appressum*	*Ophionereis reticulata*	*Ophiothrix oerstedii*	*Ophiothrix suensonii*	*Ophiocoma pumila*
	19	14	18	13	9	10	13
	18	15	13	12	7	9	9
	16	20	14	11	7	9	
	19	15	12	9	7		
	18	17	15	11	6		
	17	14	11	10	6		
	20	21	12				
	18	20	13				
	17	18	13				
	19	14	16				
No. of individuals	10	10	10	6	6	3	2
Mean disk diam.	18	17	14	11	7	9	11

light source. By observing the repeated excursions of the arms, the experimenter could fire the shutter at the approximate moment of the power stroke, during maximum curvature of the arms. After a pause of 2–3 min in darkness, the trial was repeated, for a total of 10 trials per individual. This technique is more prone to error than photography when the animal is stationary, because capturing the moment of maximum arm curvature is not guaranteed. Ophiuroid locomotion is relatively slow, however, so shutter-release errors should account for only small variations in the recorded position of the arm. Because all animals were photographed by the same experimenter (E.E.L.) under the same conditions, the tendency to err with this technique is not expected to bias comparisons among species.

Table II

Species list and ecological information

| Species	Vertebral ossicle type	Feeding mode
OPHIOCOMIDAE		
Ophiocoma echinata	non-keeled	deposit-/suspension-feeder
Ophiocoma pumila	non-keeled	deposit-/suspension-feeder
Ophiocoma wendtii	non-keeled	deposit-/suspension-feeder
OPHIODERMATIDAE		
Ophioderma appressum	non-keeled	arm-loop scavenger
Ophioderma cinereum	non-keeled	arm-loop scavenger
OPHIOCHITONIDAE		
Ophionereis reticulata	keeled	deposit-feeder
OPHIOTHRICIDAE		
Ophiothrix oerstedii	keeled	suspension-feeder
Ophiothrix suensonii	keeled	suspension-feeder
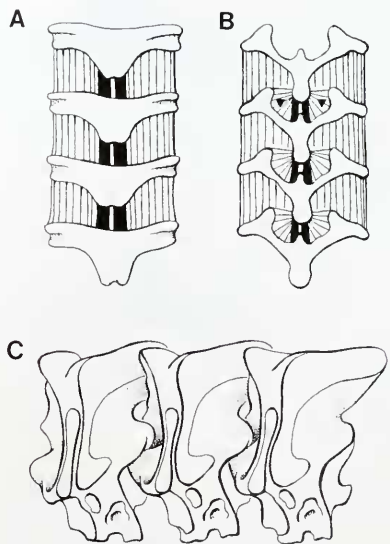
Figure 4. Dorsal views of vertebral series with external plates removed. (A) General arrangement of non-keeled vertebral ossicles (white), intervertebral muscles (striped), and dorsal ligaments (black). (B) Keeled vertebral ossicles form a nested series due to prominent aboral projections and depressions, connected by "accessory aboral muscles" (black triangles; Robbins, 1986). (C) Lateral view of a keeled vertebral series, showing overlap of adjacent ossicles within the arm.
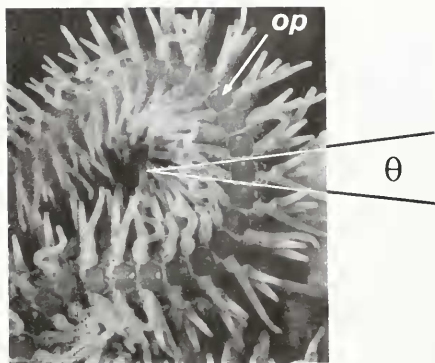
Figure 5.   Enlarged photonegative of oral arm surface, *Ophiocoma echinata*. Borders of adjacent oral arm plates were used to measure intersegmental angles (θ). op = oral plate.

to move independently of the vertebral series, the angle between adjacent oral plates cannot *consistently* be larger (or smaller) than the underlying intervertebral angle, else the oral and intervertebral series would quickly diverge. Any offset between these two series of ossicles is thus likely to be small, and unlikely to introduce any persistent bias in comparisons between species. Thus intersegmental angles, measured externally from adjacent oral plate boundaries, are probably good estimators of intervertebral rotations *in vivo.*

For each series of 10 oral plate boundaries, the digitizing program automatically calculated all intersegmental angles (θ) and the maximum intersegmental angle achieved in that region (θ_{max}). When the segments are aligned along the proximal-distal axis, θ has a value of zero; it increases to a maximum as the segments rotate.

Digitizing technique

To quantify the degree of intersegmental rotation, more than 1300 photographic negatives were digitized using BioScan OPTIMAS software (ver. 3.1). The portions of the arm with the sharpest lateral curvature were visually selected from each frame. In the locomotion experiments, the region of sharpest curvature was selected from each arm participating in the locomotory "stride." These regions were generally in the middle third of the arm, where the segments were sharply bent to push against the substrate. In the coiling experiments, the region of sharpest curvature was selected from the proximal or middle portion of each arm that appeared tightly coiled. In this treatment, there were often several tight bends per arm, and most (but not necessarily all) of the arms were involved in this form of bending.

From each selected region, line segments were digitized along the proximal borders of 10 adjacent oral plates, and the angles between adjacent plates were calculated (Fig. 5). Oral plate borders were used as landmarks for comparing segment rotations because these boundaries appeared sharpest on the photographic negatives. Because the oral arm plates are not rigidly connected to the vertebral ossicle series, we use the term "intersegmental angles" to refer to these data. Although we did not visualize the vertebral series directly, in adjacent segments the oral intersegmental angle and the underlying intervertebral angle are probably quite similar, as both series of ossicles must follow essentially the same overall arm curvature. Even if oral arm plates are free
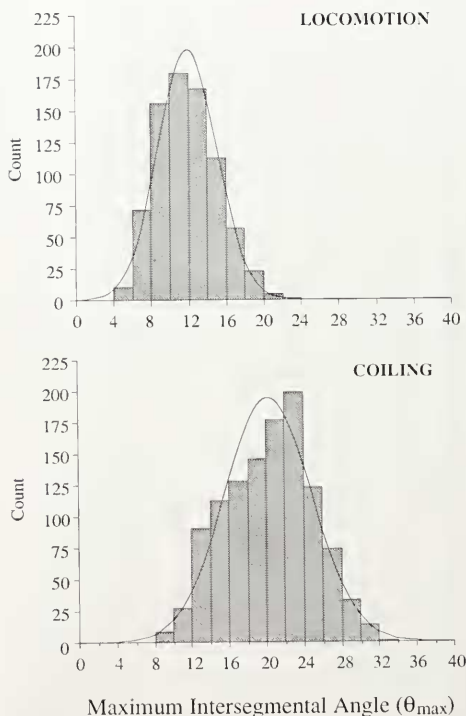

Maximum Intersegmental Angle (θ_{max})

Figure 6.   Histograms of maximum intersegmental angle (θ_{max}) for the locomotion and coiling experiments. Each histogram represents observations pooled over all species and trials. Note that the range of rotations in forced coiling is shifted upwards from the range observed for unrestrained locomotion.

The metric of interest is θ_{max}, because we wish to know whether different ophiuroid species are differently limited in their ability to flex between segments. Measurement error was determined by repetitive digitizing and was estimated to be $\pm 2°$ ($n = 900$, SD = 2.1°).

Results

Results from this photographic survey allow interspecific comparisons of *lateral* flexibility between ophiuroid arm segments. These data do not address other plausible planes of rotation, such as oral-aboral flexibility or torsion. Figure 6 compares maximum intersegmental angles pooled separately from all of the locomotion and coiling experiments. The largest intersegmental rotations were observed during coiling trials (Fig. 6B), where both the minimum and the maximum observations exceed those seen in unrestrained locomotion. This suggests that the direct illumination and limited refuge size used to elicit coiling prompts an increase in joint flexion. Because the observed rotations depend on the experimental conditions, data from the locomotion and coiling trials were analyzed separately.

Locomotion trials

Six species provided sufficient data for analysis of flexion during locomotion. Individuals within species showed similar means and variances for intersegmental angles, so all measurements from conspecifics were
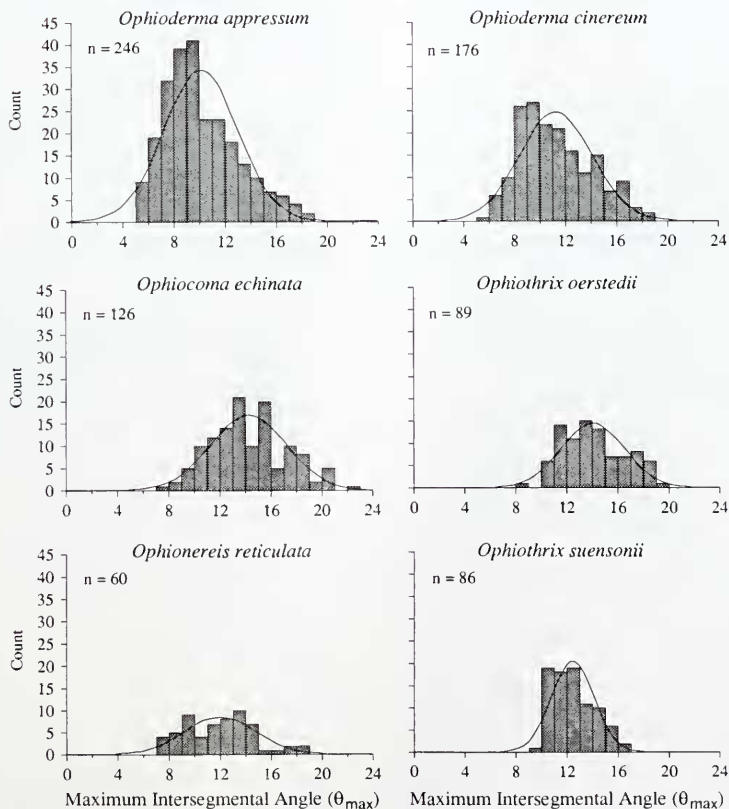

Figure 7. Histograms of maximum intersegmental angle (θ_{max}) for six Discovery Bay species photographed during free locomotion. n = number of maximal angles measured.

Species	Mean (°)	Std. Dev.	Std. Error	Min (°)	Max (°)	n
Locomotion trials						
Ophioderma appressum	10.2	2.9	0.18	5.3	18.3	246
Ophioderma cinereum	11.3	2.8	0.22	5.5	18.2	176
Ophiocoma echinata	14.3	2.9	0.26	7.3	22.3	126
Ophiothrix oerstedii	14.1	2.5	0.26	9.0	19.2	89
Ophionereis reticulata	12.0	2.8	0.36	7.6	18.9	60
Ophiothrix suensonii	12.5	1.6	0.17	9.9	16.0	86
Coiling trials						
Ophioderma appressum	17.5	3.8	0.29	9.4	27.9	168
Ophioderma cinereum	16.4	3.2	0.24	8.5	23.7	185
Ophiocoma echinata	22.1	3.1	0.19	14.4	29.4	259
Ophiothrix oerstedii	19.3	4.4	0.50	10.2	29.6	76
Ophiocoma pumila	23.1	3.0	0.34	15.9	29.8	78
Ophionereis reticulata	23.6	3.3	0.19	15.5	32.4	293
Ophiothrix suensonii	13.8	2.5	0.31	9.4	20.8	63

pooled. The resulting histograms of maximum interseg-mental angles are shown in Figure 7. Note that each spe-cies exhibits a wide range of maximum angles in lateral bending, and that among species there is considerable overlap in the range of maximum angles measured. There are small interspecific differences in the mean maximum angle, or central tendency of each range. Be-cause each distribution closely approximates a normal curve (Komolgorov-Smirnov tests, each $P < 0.05$), para-metric statistics were used to describe and compare these distributions. For multiple *post hoc* tests of the data, we used the Bonferroni correction (Rice, 1988) to adjust the within-test P value required for statistical significance.

Table III lists basic statistics for the distribution of maximal angles in each species. In lateral flexion during locomotion, most species exhibit the same range of max-imal intersegmental angles ($10° - 15°$) between arm seg-ments. Five of the six species show no significant differ-ences in variance (multiple F tests, each $P > 0.003$); the sixth species, *Ophiothrix suensonii*, is significantly less variable ($P < 0.0001$) than the others. *Ophioderma ap-pressum* and *O. cinereum* have the lowest mean rotations ($10° - 11°$), *Ophionereis reticulata* and *Ophiothrix suen-sonii* are intermediate ($\sim 12°$), and *Ophiocoma echinata* and *Ophiothrix oerstedii* show the highest mean rota-tions ($\sim 14°$). Figure 9A illustrates these differences by showing the species ranked according to mean maxi-mum angle and grouped according to significant differ-ences among means; each box encloses taxa whose means are not statistically different (multiple t tests, $P > 0.003$). Although these results show some significant interspecific differences in mean maximal rotation, the

absolute differences in this measure are small, and the functional significance of such differences is uncertain.

Coiling trials

Seven ophiuroid species are represented in the analysis of flexion during coiling. As before, maximal angles within species were normally distributed, and measure-ments from conspecific individuals were pooled. Species histograms of maximum intersegmental angles during coiling are shown in Figure 8. Each species exhibits a wide range of maximal angles, and there is considerable interspecific overlap in the maximal angles measured.

Descriptive statistics for the coiling distributions are shown in Table III. The coiling experiments tend to elicit mean lateral rotations of about $14°$ to $23°$ between arm segments. *Ophiothrix suensonii* tends to have the least rotation between segments ($13.8°$), whereas *Ophionereis reticulata* tends to have the greatest ($\sim 24°$). The conge-nerics *Ophioderma appressum* and *O. cinereum* have similar mean intersegmental angles, as do *Ophiocoma echinata* and *O. pumila*. The two species of *Ophiothrix*, however, exhibit different responses; *O. oerstedii* has an intermediate mean rotation, but the mean rotation of *O. suensonii* is rather low. Again, some interspecific differ-ences in mean maximum angle are statistically signifi-cant, as shown by a ranking of species (Fig. 9B). Note that this order of species, from the lowest mean maxi-mum to the highest, differs considerably from the order observed in the locomotion experiments (Fig. 9A). Thus the observed flexion depends not only on the species, but on the circumstances used to provoke arm flexion.

Interspecific differences in mean lateral flexibility do not clearly correspond to differences in vertebral ossicle morphology or feeding ecology. In the locomotion ex-periments, *Ophiocoma echinata* (a non-keeled, suspen-sion/deposit feeder) and *Ophiothrix oerstedii* (a keeled, obligate suspension-feeder) both share the highest mean intersegmental rotations observed (about $14°$). *Ophio-nereis reticulata* (a keeled deposit-feeder) and *Ophio-coma pumila* (a non-keeled deposit/suspension-feeder) are the most flexible species in the coiling experiments; their mean rotations ($23.1°$ and $23.5°$, respectively) are not significantly different. Thus species of different sizes, ecologies, and arm construction can achieve comparable intersegmental rotations in both of the activities mea-sured here.

Discussion

Although there are significant variations in mean in-tersegmental angles among Discovery Bay ophiuroids, the absolute angular differences are quite small, and the degree of lateral flexibility is not obviously correlated
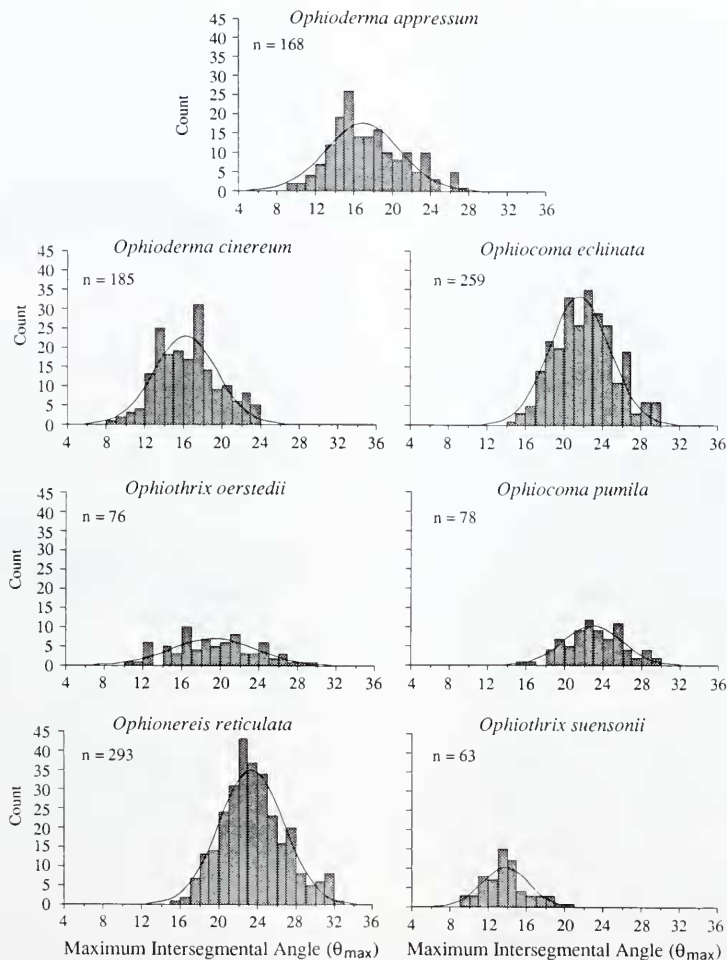
Figure 8. Histograms of maximum intersegmental angle (θ_{max}) for seven Discovery Bay species photographed while they were sheltering in a restricted space (= "coiling"). n = number of maximal angles measured.

with vertebral form or trophic mode. These data contrast with previous studies that have claimed mechanical significance for small interspecific variations in vertebral ossicle morphology. We tested this assumption by comparing species with non-keeled vertebral ossicles (*Ophiocoma, Ophioderma*), and species with keeled vertebral forms (*Ophionereis, Ophiothrix*). If these two vertebral types differ greatly in their capacity for lateral bending,

we might expect to see species from one group consistently out-bend those of the other.

The observed differences among ophiuroid species are more complex, as shown in a summary of the angular measurements (Fig. 10). First, the overall *ranges* of maximal rotations exhibited by different species greatly overlap. Second, a high *mean* maximal rotation is not confined to species of a particular vertebral type or feeding

strategy. Third, although the difference among means is significant for some species, the groups formed by this quantitative criterion do not clearly separate species according to either morphology or general ecology.

Species vary not only in their *mean* rotations, but also in the apparent *extremes* of rotation (Fig. 10). The largest single deflection between arm segments (32.4°) was observed in *Ophionereis reticulata* during coiling (Table III). This amount of lateral rotation is only slightly greater than that observed in *Ophiocoma pumila* (29.8°), *Ophiothrix oerstedii* (29.6°), and *Ophiocoma echinata* (29.4°) under the same conditions. Other species in this trial show much lower extremes, *i.e.*, *Ophiothrix suensonii* (20.8°).

Though one might interpret these extreme values as species-specific "limits" on intersegmental flexibility, several caveats apply. (For a recent treatment of extremes in ecology, see Gaines and Denny, 1993.) As in any behavioral study, we can measure only the "actual" or observed performance of adjacent segments, not the "potential" performance of which they are theoretically capable. Actual intersegmental rotations clearly depend on experimental circumstances; nearly all species show greater rotations in the coiling trials, and some increase flexion more than others. *Ophiocoma pumila* and *Ophionereis reticulata* seemed particularly sensitive to this treatment, vigorously retracting their arms into multiple loops and
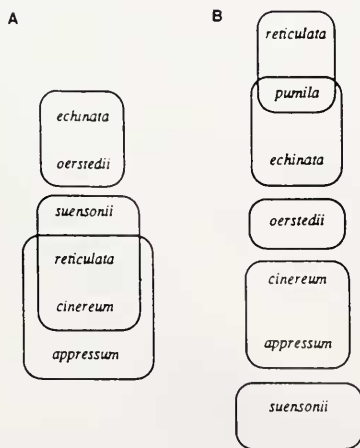

Figure 10. Boxplots comparing the range of maximum intersegmental angle (θ_{max}) for species in the locomotion (A) and coiling (B) experiments.

Figure 9. Graphical presentation of *t* test results. Species are ranked by mean maximum intersegmental angle (θ_{max}) from highest (at top) to lowest (at bottom). Each box encloses species whose means are not significantly different. (A) Locomotion trials, $P < 0.0033$. (B) Coiling trials, $P < 0.0023$.
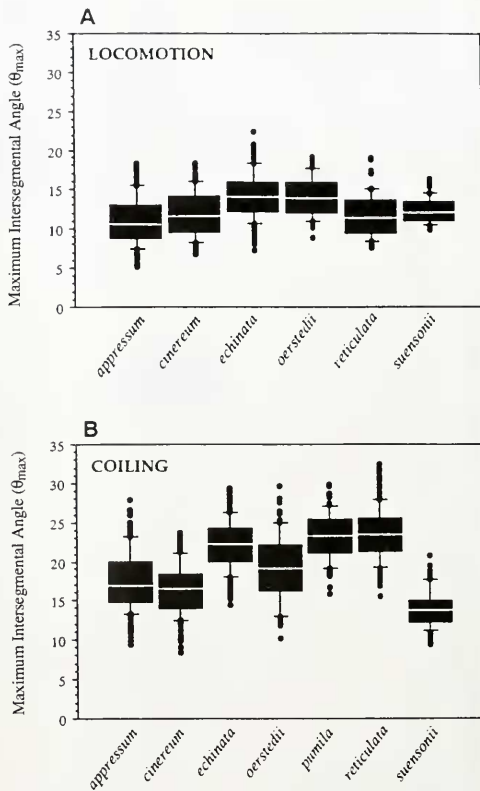
coils. The single species that is exposed during daylight (*Ophiothrix suensonii*) shows the least change between experimental treatments. These behavioral variations may confound comparisons of musculoskeletal performance, even when ophiuroids perform the "same" activities. For two species under the same conditions, actual bending may be close to the potential limit in one, but not in the other. Despite these limitations, our quantitative data suggest that there is nothing inherently limiting in either type of ophiuroid vertebral ossicle: within each treatment, species with keeled and non-keeled morphologies can achieve similar extremes of lateral rotation.

The lack of correspondence between vertebral form and maximal intersegmental angles in these species argues against the notion that vertebral morphology is a

dominant factor in limiting intersegmental rotation. As others have suggested, there is likely to be a complex interaction between the intervertebral articular surfaces, the external plates, and associated soft tissues in the ophiuroid arm (for review, see Byrne, 1994). Biomechanical influences on intersegmental rotation may include the extensibility of the integument (Byrne and Hendler, 1988), the neurally mediated stiffness of the connective tissue (Wilkie, 1978, 1979, 1992), the arrangement of the intervertebral musculature (Emson and Wilkie, 1982), and the conformation of the external arm plates (Litvinova, 1994). For example, Litvinova (1994) recognizes 15 types of ophiuroid arm structure on the basis of the size and shape of the external plates and their overall pattern of contact. These plate configurations are divided into three groups: those that "do not restrict," those that "slightly restrict," and those that "strongly restrict" arm movements. This classification, like most functional discussions of the ophiuroid vertebral system, seems to presuppose that there are inherent, species-specific differences in the capacity for intersegmental rotation.

Although we found no outstanding differences in intersegmental flexibility among the ophiuroids in our sample, this study is limited to the measurement of lateral flexion. The vertebral variants tested here may somehow contribute to interspecific differences in the range of dorsoventral bending or torsion. Until such differences can be measured, however, we must be more skeptical of the notion that vertebral ossicle morphology dictates flexibility between segments, and less speculative about how some types of segments are more (or less) flexible than others. If interspecific variation in intersegmental flexibility is more apparent than real, the present functional diversity of the Ophiuroidea cannot be explained solely by the evolutionary accumulation of vertebral ossicle variations that modify joint biomechanics. The ecological breadth of ophiuroids may be due to many combined factors of arm construction, including segment size; segment number; the control of muscles and mutable collagenous tissues; and the behavioral coordination of accessory spines, scales, and tube feet. The tendency to link vertebral variation with higher-level ecology in these animals is also at odds with several vivid accounts of how species can be ecologically labile, facultatively assuming three or four feeding modes (Fontaine, 1965; Fell, 1966; Reese, 1966; Magnus, 1967; Pentreath, 1970; Woodley, 1975; Feder, 1981). An alternative hypothesis is that vertebral ossicle morphology is variable because it has little or no influence on intersegmental rotation, and does not affect how (or how well) the ophiuroid makes its living.

Diversity in the external aspect of the skeleton has been the foundation of ophiuroid taxonomy. Diversity in the internal skeleton remains poorly understood both in its morphological variance and in its functional effects. Although keeled and non-keeled ossicles are the major vertebral variants in these epifaunal species, other ophiuroid families show even more diverse arm morphologies and lifestyles. These include infaunal amphiurids (which have extremely long, slender arms), epifaunal hemieuryalids (which have highly flexible, coiled grasping arms with a streptospondylous articulation), and the enigmatic ophiomyxids (which have a reduced axial skeleton and large amounts of connective tissue; see Byrne and Hendler, 1988). These groups are open for the further testing of form-function relationships.

Although the ophiuroid axial skeleton is conspicuously variable in morphology and obviously functional in its anatomical role, at the mechanical level we know little about how morphological variations influence intersegmental flexibility. At the ecological level, we lack convincing arguments to link flexibility *per se* to the style or success of an ophiuroid's locomotory or food-gathering movements. Further work must establish what are the differences in intersegmental flexibility, if any, among ophiuroid species, and in what way these differences are meaningfully correlated with ecologically relevant behaviors. More detailed behavioral visualization, mechanical testing of individual arm segments, and physiological recording of muscle activity may further elucidate the range and response of the intersegmental junction. Future discussions of the vertebral ossicle system should also make clear whether physical capabilities or biological roles are implied when skeletal morphology is described in functional terms (Gans and Gasc, 1992). Although ophiuroids are "flexible in feeding habits" (Fontaine, 1965) as well as flexible in motion, these two flexibilities may be only distantly related.

Acknowledgments

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